POLLEN STUDIES IN RELATION TO HYBRIDIZATION IN CERCIDIUM AND PARKINSONIA (LEGUMINOSAE: CAESALPINIOIDEAE)

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During a study of *Cercidium* in the Sonoran Desert (Carter, 1974a; 1974b), the hypothesis was developed that *Cercidium sonorae* is of hybrid origin and that the parental species are *C. microphyllum* and *C. praecox*. The hybrid is known to occur only within the distributional overlap of these two species.

Because interspecific hybrids commonly exhibit reduced fertility as compared to parents, and since pollen fertility may be studied by staining pollen with aniline-blue lactophenol ("cotton blue", Hauser and Morrison, 1964), pollens from samples of *C. sonorae* were tested for relative fertility. For comparative purposes, the examination of pollen was extended to include other taxa of *Cercidium* and the related genus *Parkinsonia*. Percentages of stained pollens reported in Table 1 and in the following discussion are based on samples of mostly 300 to 600 (200 to 1250) pollen grains per collection. Pollen of the *species* studied showed stainabilities of 83 to 98 percent, whereas pollen stainabilities in various *putative hybrids* varied from 5 to 76 percent (except in *Kamb 2014*).

In those specimens of *Cercidium sonorae* examined for presumed pollen viability, the percent of stained pollen varied from 42 to 76 percent, whereas in the putative parents, *C. praecox* and *C. microphyllum,* 89 percent or more of the pollen stained with cotton blue. One exception (*Carter & Ferris 3446* with 84 percent of the pollen grains stained) is not typical *C. microphyllum* and the tree may represent a backcross between *C. sonorae* and *C. microphyllum*. The morphological characters in which *C. sonorae* resembles or is intermediate between one or the other of its putative parents are set forth elsewhere (Carter, 1974a).

Pollen stainability in a putative hybrid between *Cercidium floridum* and *C. microphyllum (Kamb 2014* from near Sierra Pinacate, northern Sonora) is 86 percent. The specimen has leaflets larger than typical for *C. microphyllum* and more leaflets than usual in *C. floridum;* pubescence of the ovary is similar to that in *C. microphyllum;* the thorns are comparable to those in *C. floridum*. Both of the putative parents are known to occur in the area (Hastings, Turner, and Warren, 1972); in fact two sheets (DS, UC) of the Kamb collection contain branches of *C. floridum* bearing immature legumes, as well as the flowering branch of the putative hybrid; a third sheet (ARIZ) bears only a fruiting branch of *C. floridum*.

Discovery of a putative hybrid between *Cercidium praecox* and *Parkinsonia aculeata* is an interesting story. During the course of a field trip

TABLE 1. COMPARISON OF POLLEN STAINABILITIES AND SIZES IN CERCIDIUM AND PARKINSONIA AND THEIR PUTATIVE HYBRIDS. Unless otherwise noted, all collections are from Baja California Sur, Mexico, and are in the Herbarium of the University of California, Berkeley. Duplicates of the Carter, and Carter et al. collections are to be distributed.

Collection	Percent stained	Pollen size in micrometers Range	Mean
Cercidium floridum Benth. ex Gray			
Munz & Hitchcock 12166: 20 mi. NE of Ogilby, Imperial Co., Calif. 6. IV. 1932.	96	24.7–29.9	27.0
Carter 4359: plain N of Empalme, Sonora, 6. IV. 1962.	98	24.7–28.6	26.9
Cercidium macrum Johnston			
Palmer 125: vicinity of Victoria, Tamaulipas, in 1907.	97	Not measured.	
Cercidium microphyllum (Torr.) Rose & Johnston			
Carter & Ferris 3446: Rancho Aguajito, Arroyo Gua, N of Loreto, 24.IV.1955.	84	23.4–27.3	25.1
Carter 4415: Rancho La Venta, 16 km W of Loreto, 21.IV.1962.	99	23.4–28.6	25.6
Carter 5670: 55 km E of Villa Insurgentes, 3. V.1972.	89	24.7–28.6	26.5
Cercidium peninsulare Rose			
Carter 2595: Arroyo del Salto, E of La Paz, 30.III.1949.	85	23.4–28.6	25.7
Carter 4414: San Javier, W of Loreto, 21.IV. 1962.	91	22.1–27.3	25.2
Carter & Reese 4537: San Bruno N of Loreto, 1.VI.1963.	89	23.4–27.3, 32.5–33.8	26.5
Carter 5680: Rancho Viejo, 39 km from Loreto on road to San Javier, 6.V.1972.	87	22.1–26.0	24.7
Cercidium praecox (Ruiz & Pavón) Harms			
Carter & Ferris 4046: Cuesta de los Encinos, SE of Cerro Giganta, 29.III.1960.	95	22.1–26.0	23.7
Carter, Hastings & Turner 5576: Los Hoyos, northeastern Sonora, 23.IV.1971.	96	20.8–24.7	22.8
Cercidium sonorae Rose & Johnston (putative parents are *C. microphyllum* and *C. praecox*).			
Johnston 3877: Agua Verde Bay, 26.V.1921 [isotype of *C. molle* Johnston].	52	22.1–26.0	24.2
Carter 5610: Bahía Agua Verde, 23.VIII. 1971.	42	19.5–26.0	22.5
Carter, Hastings & Turner 5595: Guaymas to Hermosillo Highway, 0.6 mi N of Bahía San Carlos junction, Sonora, 2.V.1971.	45	22.1–27.3	24.5
Carter 5679: San Javier, W of Loreto, 6.V.1972.	76	18.2–24.7	22.6
Cercidium texanum Gray			
Hedrick 258: ca 8 mi SW of Spofford, Kinney Co., Texas, 17.IV.1940.	83	Not measured.	

TABLE 1. *Continued*

Parkinsonia aculeata L.			
Hinton 5642: Coyuca, Guerrero, 16.II.1934 (ARIZ, MEXU).	95	23.4–29.9	27.5
Carter 4413: San Javier W of Loreto, 21.IV. 1962.	98	26.0–31.2	29.6
Unnamed putative hybrid collections.			
Putative parents: *C. floridum* and *C. microphyllum:*			
Kamb 2014: Molina Crater, NW of Sierra Pinacate, Sonora, 29.IV.1951 (DS, UC).	86	22.1–27.3	25.0
Putative parents: *C. praecox* and *Parkinsonia aculeata:*			
Hinton 6040 Coyuca, Guerrero, 11.V.1934. (BM, NY).	20	22.1–27.3	24.3
Hinton 9968: Coyuca, Guerrero, 25.III.1937 (ARIZ, BM, K, MEXU, NY).	21	20.8–28.6	25.4
Carter, Hastings & Turner 5575: Los Hoyos, northeastern Sonora, 23.IV.1971.	21	20.8–33.8	28.7
Putative parents: *Cercidium* sp. and *Parkinsonia aculeata:*			
Vines 142: 6 mi NW of Brownsville, Texas (US).	28	22.1–28.6, 32.5–33.8	24.8
Bone in 1972, Zapata Co., Texas (TEX).	5	20.8–28.6	24.2

in northeastern Sonora with J. R. Hastings and R. M. Turner in the spring of 1971, the senior author collected flowering material from a large tree near the small pueblo of Los Hoyos (lat. 30° 06′ N, long. 109° 48′ W). At the time, we considered it to be a particularly verdant tree of *Cercidium sonorae* although the collection site was more than a degree distant, in latitude and longitude; from the nearest known locality for that taxon (Hastings, Turner, and Warren, 1972). Both *Cercidium praecox* and *Parkinsonia aculeata* were growing in the vicinity and were in full flower. Subsequently, on studying the material of this collection *(Carter, Hastings, & Turner 5575),* it was found that the specimens exhibited certain characteristics of *Parkinsonia aculeata* (cf. Table 2). Inasmuch as both putative parents have pollen stainability of 95 percent or more, the low pollen stainability of 21 percent for this tree served to confirm the hypothesis that it was of hybrid origin. In July of the same year, Hastings returned to Los Hoyos in the hope of collecting mature legumes. He found a cleared field where the thorn-scrub vegetation had been, and only the stump of the tree remained! Extensive search in the area failed to reveal any trees comparable to the one that had been cut down. Later that year, while studying the holdings of *Cercidium* at the Instituto de Biología, Universidad Autónoma de México, the senior author noted a specimen from Coyuca, Guerrero, México,

Table 2. Comparison of Morphological Characteristics in Selected Samples of Cercidium praecox, Parkinsonia aculeata, and Their Putative Hybrids. Collections studied. *Cercidium praecox: Moore, Hernández X., & Porras H. 5765,* rocky plain ca 11.4 km from Tepalcatepec, on road to Apatzingán, Michoacán, 15.XI.1949 (in leaf only). Putative hybrids: a) *Hinton 9968,* and b) *Carter, Hastings & Turner 5575* (in flower only), collection data given in Table 1. *Parkinsonia aculeata: Hinton 5642,* collection data given in Table 1. Statements and figures enclosed in brackets are based on a series of specimens in addition to those cited. The symbol x indicates average.

Character	*Cercidium praecox*	Putative hybrids	*Parkinsonia aculeata*
Armature	one [or two] stout thorns (undeveloped branchlets) in axil of first leaf at a node	lacking	indurate petiole and rachis of first leaf developing at a node terminates in a sharp, stout spine; petiole also often bears stout, often recurved stipular spines
Petiole length (mm)	3.0–8.5; x=6.2 [(1–) 411(–21); x=7.6]	a) 1.5–3.5; x=2.4 b) 1.4–6.0; x=3.2	ca. 0.5–6.0; x=1.4
Pinnae	not phyllodial, orbicular in cross section	not phyllodial, somewhat flattened but not winged	phyllodial, flat and narrowly or broadly winged
length (cm)	0.6–1.4; x=1.0 [0.4–4.5; x=1.7]	a) 4.5–7.5; x=6.2 b) 3–11; x=7.9	8–29; x=19.6
width (cm)	0.3–0.8; x=0.4	a) 0.4–0.8; x=0.6 b) 0.4–0.6; x=0.4	3–4; x=3.3
Leaflets	opposite, not caducous	opposite and/or alternate, ± caducous	opposite and/or alternate, caducous
number (on one side of pinna)	4–7 [3–17]; x=5.8 [6.5]	a) 11–20; x=14.1 b) 8–20; x=15.5	19–38 [10–40]; x=29.4
spacing	5–6/cm; x=5.6	a) 2–3/cm; x=2.2 b) 2/cm	1–2/cm; x=1.5
length (mm)	3.2–4.8; x=4 [3–8; x=5.9]	a) 3.4–8.0; x=6.9 b) 4–5; x=4.4	1.6–2.0; x=1.8
width (mm)	1.6–2.0; x=1.7	a) 1.2–3.4; x=2.0 b) 1.2–2.2; x=1.6	0.4–0.6; x=0.5
Inflorescence	[borne in usually compact clusters along mature branches and developing ahead of leaves]	a and b) open racemes on terminal and subterminal branches; developing with the leaves and equaling or exceeding the pinnae	open racemes on terminal and subterminal branches; developing with the leaves and shorter than the pinnae

TABLE 2. *Continued*

peduncle length (mm)	[0.1–6.4; x=1.9]	a) 4–13; x=8.6 b) 3–25; x=14.7	10–20; x=16
plus rachis (cm)	0.1–2.0; x=0.9	a) 1–27; x=18 b) 3.4–11.5; x=7.6	4.8–17.0; x=10.8 [6.9–23.5; x=15.0]
Legume vestiture at anthesis	glabrous	a and b) glabrous or with a few strigose hairs	strigose
mature	flat and papery; net-veined; not or scarcely constricted between seeds; indehiscent	a) flat and papery; net-veined; not or scarcely constricted between seeds; indehiscent	thin-walled; enlarged over the seeds and constricted between them; longitudinally striate but veins somewhat anastomosed; irregularly dehiscent
length (cm)	[3.0–5.7; x=4.3]	a) 3.5–6.7; x=4.5	2.5–6.0; x=4.7 [3.0–13.5; x=7.2]
Seeds (number)	[1–3; x=1.4]	a) 1–2	1–4; x=1.6 [1–6; x=2.8]

(Hinton 9968) having vegetative characters similar to those of our Los Hoyos collection. It bore mature legumes resembling those of *C. praecox* and it had been so identified at Kew. Subsequently, in other herbaria, additional Hinton collections of this putative hybrid were noted. Their low pollen stainability of 20 percent is comparable to that of the Los Hoyos specimen. Both *Cercidium praecox* (*Hinton 5455,* US) and *Parkinsonia aculeata* (*Hinton 5642,* ARIZ) are known to occur in the vicinity of Coyuca. Comparison of these putative hybrids and their presumed parents is made in Table 2. The yellow, structurally similar caesalpinioid flowers of *Parkinsonia aculeata* and *Cercidium praecox* exhibit the same ultra-violet light absorption pattern, i.e., the median (posterior) petal is strongly absorptive and thus appears dark or "bee-purple" under ultra-violet light and the other four petals reflect ultra-violet light. In occasional specimens all five petals of *C. praecox* absorb ultra-violet light (Carter, 1974a). Field studies, such as those that Jones (pers. comm., California State University, Fullerton) has done on *C. microphyllum* and *C. floridum,* should be carried on to determine habits of the bees visiting *Parkinsonia* and *Cercidium.*

Two specimens from Texas (*Vines 142,* US, and *Bone* in 1972, TEX), which also appear to be of hybrid origin, have been referred to the senior author. Unfortunately, no field data are available as to species associ-

ated with the Bone specimen; the label on the Vines specimen states, "Growing with *Cercidium* and *Parkinsonia* in hard, dry soil; shrub 12 feet high." On the basis of morphological characters and low pollen stainability (Table 1), it is suggested that they resulted from hybridization between one of the two Texas species of *Cercidium (C. texanum* or *C. macrum)* and *Parkinsonia aculeata.* The Vines specimen, with a pollen stainability of 28 percent, is similar in appearance to the putative hybrids from Guerrero and Sonora *(P. aculeata* × *Cercidium praecox)* except that the apex of the petiole is subspinescent. The Bone specimen, with only five percent stainable pollen, has shorter pinnae than the Vines specimen, opposite leaflets, and subspinescent petiole tips. Neither specimen bears any axillary thorns. The Vines specimen is in flower only, but the ovary is strigose, as it is also in *Parkinsonia aculeata* and *Cercidium texanum.* In the Bone specimen the ovary is only slightly pubescent, but the one-seeded mature legumes resemble those of *P. aculeata* in texture and venation of the valves and in being somewhat enlarged around the poorly developed seed.

Pollen of *Parkinsonia aculeata* and of the species of *Cercidium* dealt with in this study show little difference in shape under the light microscope whether unstained and acetolyzed (Erdtman, 1952, p. 6) or stained with aniline-blue lactophenol. The grains are prolate spheroidal, tricolpate, and supra-reticulate (Erdtman, 1952; Faegri and Iversen, 1964).

As seen under the scanning electron microscope, however, the general shape of the grains is different; drying and coating of the grains results in partial collapse and therefore the equatorial diameter is greatly reduced (fig. 1). Again, all except the *Parkinsonia aculeata* × *Cercidium praecox* putative hybrids are similar to each other in appearance, but the number of granules (verrucae) within the lumina varies. This is especially noticeable in *Cercidium microphyllum* (fig. 1, c) and *Parkinsonia aculeata* (fig. 1, f); pollen from a series of specimens should be studied, however, to determine whether or not this difference between the two is constant. In pollen of other *Cercidium* taxa observed under the scanning electron microscope, the number of these granules is somewhat variable, even on a single pollen grain. Martin and Drew (1969; 1970), in their survey of southwestern pollen grains by means of the scanning electron microscope, included *Cercidium floridum, C. microphyllum,* and *Parkinsonia aculeata.* They state that pollen of *P. aculeata* differs from that of *Cercidium* in its relatively smaller lumina and heavier muri. There is apparently variation in these characters inasmuch as the material seen in this and a subsequent study (Carter, 1974b) does not display such differences. In *C. sonorae,* the putative hybrid between *C. microphyllum* and *C. praecox,* there are almost no aberrant-shaped pollen grains even though *C. sonorae* pollen exhibits only 42 to 76 percent staining with cotton blue. In the putative hybrid between *C. floridum* and *C. microphyllum (Kamb 2014),* also, the number of

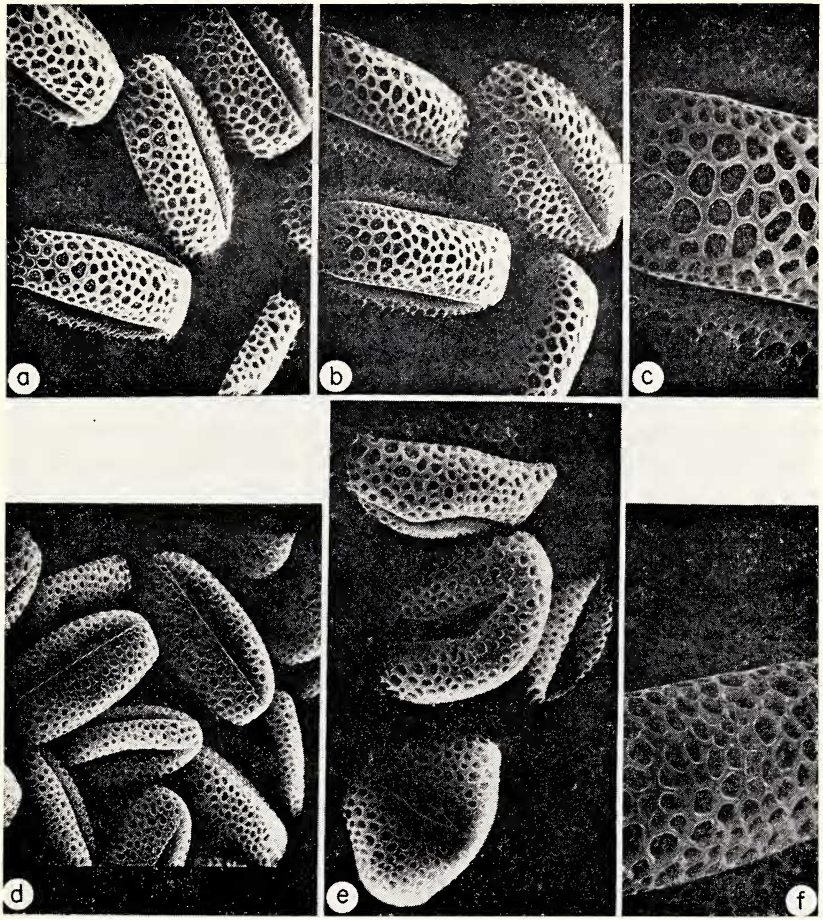

FIG. 1. Pollen of *Cercidium* and *Parkinsonia* as seen under the scanning electron microscope. *a, Cercidium praecox (Carter 5576),* ca × 1000; *b, C. microphyllum (Carter 5675,* 1 km W of Las Parras summit on road from Loreto to San Javier, Baja California Sur, 6.V.1972), ca × 1000; *c,* the same, × 2000; *d, C. sonorae (Carter 5679),* ca × 750; *e,* putative hybrid between *C. praecox* and *Parkinsonia aculeata (Carter, Hastings & Turner 5575),* ca × 750; *f, Parkinsonia aculeata (Carter 5666,* near km 112, NW of La Paz on highway to Villa Constitución, Baja California Sur, 3.V.1972), ca × 2000. Collection data not included above are given in Table 1. The photographs were taken at the Electronics Research Laboratory, University of California, Berkeley.

aberrant grains is minimal. On the other hand, in the putative hybrids between *C. praecox* and *Parkinsonia aculeata,* with only 20 to 21 percent presumably viable pollen, there is a high percentage of malformed pollen (fig. 1, e) as is also the case with the two putative hybrids from Texas.

Pollen size may be affected by so many factors (Bell, 1959; Muller,

1969, p. 228) that its use as a diagnostic taxonomic character is not feasible here. In hybrids, however, variation in pollen size may be significantly greater than in species, e.g., in the *Parkinsonia-Cercidium* hybrid *(Carter, Hastings, & Turner 5575)* variation in pollen size is much greater than in any other taxon measured. Pollen sizes in the Sonoran Desert taxa treated, as examined under the light microscope are included in Table 1. Measurements were taken from unmistakably blue-stained grains. The range in size of pollen grains in two specimens *(Carter & Reese 4537, C. peninsulare; Vines 142, Parkinsonia aculeata* × *Cercidium* sp.) is striking in that a few of the grains are unusually large (32 to 34 μm), and there are no grains of intermediate sizes between those and the normal group measuring 28 μm or less. In the Carter and Reese specimen only 1.7 percent of the grains measured are of the abnormally large size and in the Vines specimen, 8.2 percent. These large grains are included in calculating means.

Conclusions

That *Cercidium sonorae* has a much lower percent pollen stainability than do its putative parents, *C. microphyllum* and *C. praecox,* substantiates morphological evidence as to its hybrid origin.

The paucity of putative hybrids between species of *Cercidium* and *Parkinsonia aculeata,* the extremely low percent pollen stainabilities in such hybrids as have been noted, and the high percent of malformed pollen grains in such putative hybrids suggest that *Parkinsonia aculeata* is not as closely related to *Cercidium* as the taxa included in *Cercidium* (Johnston, 1924; Carter, 1974b) are related to each other.

Acknowledgments

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NOTES AND NEWS

New Distribution Records of Mosses in California.—*Buxbaumia piperi* Best. Only two collections of the seldom seen *B. piperi* have been reported from California, one from northern Humboldt County, the other from southwestern Siskiyou County by Jamieson and Holmberg (Bryologist 72:72–73. 1969). In November, 1971, a small colony of *B. piperi* was discovered by Dennis Fordham and the authors on a burned redwood stump bordering a lily pond at Mendocino Woodlands Camp, 20 km east of Mendocino, Mendocino County. A year later, numerous boat-shaped sporophytes were collected from the same stump and from adjacent exposed roots in a roadcut. These collections extend the southernmost range of the species approximately 232 km. California: Mendocino Co., *Toren 613*.

Grimmia mariniana Sayre. This species, restricted to California, has been recorded only from the type locality on the summit of Mt. Tamalpais, Marin County, elevation 776 m, by Sayre (Bryologist 58:323–325. 1955), and from Mt. St. Helena, Napa County. In April, 1972, a third population was found at the summit of Hull Mountain in the extreme northern portion of Lake County. The colonies occurred in an open Red Fir forest at an elevation of 273 m on exposed, south-facing sandstone where snow accumulates and often persists until mid-April. This population at Hull Mountain extends the range of the species northward approximately 100 km from Mt. St. Helena and indicates that *G. mariniana* occurs in a wide range of habitats. California: Lake Co., *Toren 779*.

Grimmia occidentalis Lawt. In the spring of 1973, this semi-aquatic moss was found on serpentine rock in a creek at the State Game Refuge 2A near Lake Pillsbury, Lake County. This high elevation species was reported by Lawton at 2286–2590 m (*Moss flora of the Pacific Northwest,* Hattori Botanical Laboratory, Nichinan, Japan. 1971). However, the authors found it growing at the low elevation of 914 m, a phenomenon observed in other plant species on serpentine. Formerly reported from Wyoming, Montana, Nevada, and two localities in California, this collection extends the range of *G. occidentalis* southward from Lassen County to the Coast Ranges of Lake County. California: Lake Co., *Toren 860, Sigal 63*.

Grimmia heterophylla Kindb. ex Macoun & Kindb. The discovery of a well established population of this species represents a new addition to the moss flora of California. The plants were growing in loose, fragile tufts on vertical, calcareous sandstone cliffs in an exposed habitat at Hell's Peak, Lake County, at an elevation of 610 m. In association with *Grimmia heterophylla* were the other common species *G. laevigata, G. pulvinata,* and *G. montana*. This species has previously been recorded from British Columbia, Washington, and Idaho by Lawton (op. cit.). California: Lake Co., *Toren 778*.

The collections of the authors are in the herbarium at California State University, San Francisco. We wish to thank Dr. Daniel Norris for assistance in determining *Grimmia mariniana* and *G. heterophylla*.—David Toren and Lorene L. Sigal, Department of Ecology and Systematic Biology, California State University, San Francisco 94132.